

Unusual tetrapod teeth from the Upper Triassic Chinle Formation, Arizona, USA¹

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Abstract: Two teeth collected from the Upper Triassic Chinle Formation of northeastern Arizona are described here and named *Kraterokheirodon colberti* gen. et sp. nov. These teeth are novel in having an occlusal ridge with six cusps and a posterior shelf lacking dentine. Evidence for thecodont implantation of the root suggests amniote affinities for these teeth. They do not match any teeth known for basal vertebrates or basal tetrapods. Although the teeth display some affinities with “traversodont” cynodonts, there are significant differences that preclude a referral to this group. These teeth most probably represent an unknown tetrapod clade and document the presence of a large amniote previously unknown from Late Triassic terrestrial faunas.

Résumé : Deux dents provenant de la Formation de Chinle du Trias supérieur du nord-est de l'Arizona sont décrites et attribuées à *Kraterokheirodon colberti* gen. et sp. nov. Ces dents sont uniques en cela qu'elles présentent une crête occlusale dotée de six cuspides et un plan de morsure postérieur exempt de dentine. Des observations à l'appui d'une implantation thécodonte de la racine laissent croire à des affinités avec les amniotes. Ces dents diffèrent de toute autre dent attribuable à des vertébrés primitifs ou des tétrapodes primitifs. Bien qu'elles présentent certaines affinités avec les cynodontes « traversodontes », d'importantes différences écartent leur affectation à ce groupe. Ces dents représentent vraisemblablement un clade de tétrapodes inconnu et témoignent de la présence d'un grand amniote, jusqu'ici inconnu, dans les faunes terrestres du Trias tardif.

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Introduction

In 1946, G.E. Hazen of the US. Geological Survey collected a large, complex tooth from the Chinle Formation southeast of St. Johns, Arizona, and later gave it to Dr. Edwin H. Colbert of the American Museum of Natural History for study (Long and Murry 1995). Subsequently, in 1984, Lynette Gillette collected a similar large tooth from the Chinle Formation of Petrified Forest National Park, in northeastern Arizona. Dr. Colbert started study of these teeth, but passed away before the completion of his research. The only published records are two faunal lists in Murry and Long (1989) and Long and Murry (1995), assigning the Petrified Forest tooth to a “traversodont” cynodont. Here, we describe both teeth and discuss their possible phylogenetic affinities.

Institutional abbreviations

AMNH, American Museum of Natural History, New York, N.Y., USA.

PEFO, Petrified Forest National Park, Arizona, USA.

Geologic Setting

The first tooth, AMNH 4947, was collected from an exposure of the Upper Triassic Chinle Formation 5 km southeast of the town of St. Johns, Arizona (Fig. 1). In ascending order, the Chinle here consists of Shinarump, Bluewater Creek, and Blue Mesa members (Fig. 2) (Stewart et al. 1972; Heckert and Lucas 2003). These sediments unconformably overlie the Lower–Middle Triassic Moenkopi Formation. It is unclear exactly which outcrop the specimen was collected from, and thus precise stratigraphic placement is not possible. However, the tooth was probably collected from either near the base of the Blue Mesa Member (sensu Woody 2003) or near the top of the Bluewater Creek Member, as both members are present in the immediate vicinity. They are composed primarily of fluvial sediments, with the Blue Mesa Member dominated by overbank mudstones with some channel sandstones (Woody 2003).

Dating of this portion of the Chinle Formation is possible through both vertebrate and palynofloral biostratigraphy. The

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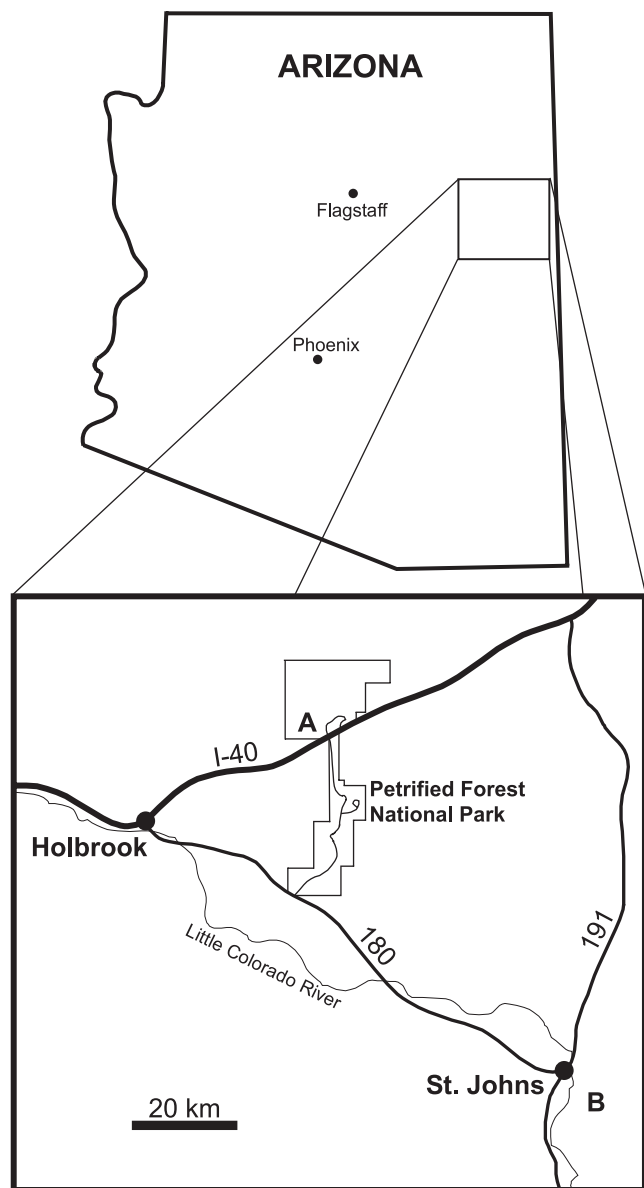
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Fig. 1. Locality map for specimens discussed within the text. (A) Locality for PEFO 9984 within Petrified Forest National Park and (B) locality for AMNH 4947 southeast of St. Johns.



vertebrate fauna from the *Placerias* Quarry and the Blue Hills in and around St. Johns indicates a late Carnian age (Adamanian land-vertebrate faunachron of Lucas 1998) for the strata (Lucas 1993; Lucas and Hunt 1993; Lucas et al. 1997). Although the St. Johns's sediments have never been analyzed palynologically, correlative and immediately overlying strata of the Chinle Formation in Petrified Forest National Park to the north have produced an unambiguous late Carnian date (Litwin 1986; Litwin et al. 1991). Recent calibration of the chronostratigraphic divisions of the Triassic Period suggests a date of between 217–225 Ma for the late Carnian (Kent and Olsen 1999).

The second tooth, PEFO 9984, was collected from site PFV 34, in the Painted Desert region of Petrified Forest National Park (Fig. 1). Although the fauna at PFV 34 is not

complete enough to use for vertebrate biostratigraphy, this locality is approximately 200 m north of and stratigraphically equivalent to PFV 40, which is a richly fossiliferous site known as “Dinosaur Hill” (Parker 2002 and references therein). Both of these localities are located within the Petrified Forest Member (Fig. 2) (sensu Woody 2003). Within the member, they are stratigraphically approximately 50 m below the Black Forest Bed (Heckert and Lucas 2002), a locally extensive reworked tuff layer (Ash 1992).

The vertebrates from PFV 40 and PFV 34 both unambiguously indicate an early-to-middle Norian (Revueletian land-vertebrate faunachron of Lucas 1998) age for the strata (Lucas and Hunt 1993; Lucas 1998). Key taxa present at both sites include pseudopalatine-grade phytosaurs, the aetosaur *Typothorax coccinarum*, and abundant fossils of the metoposaurid amphibian *Apachesaurus gregorii*. Palynological samples from correlative sediments within the park indicate an early Norian age (Litwin 1986; Litwin et al. 1991). Chinle sediments that overlie the Petrified Forest Member in Utah and north-central New Mexico have a palynoflora that only suggests that they are younger than Carnian and older than latest Norian in age (Litwin et al. 1991). This provides little constraint for the age of the top of the Petrified Forest Member. Fortunately, the only known layer within the Chinle Formation that can be radiometrically dated is the aforementioned Black Forest Bed. A new date using U–Pb radioisotopes from zircon crystals has yielded a maximum date for the Black Forest Bed of 213 Ma, with a date of 209 Ma being preferred by the authors (Riggs et al. 2003). This is consistent with a mid-Norian age based on the recent calibrations of the Late Triassic time scale (Kent and Olsen 1999). In summary, the St. Johns tooth is late Carnian in age, while the Petrified Forest specimen is probably early to middle Norian in age.

Systematic paleontology

Vertebrata Linnaeus, 1758

Tetrapoda Goodrich, 1930

Amniota incertae sedis Haeckel, 1866

Kraterokheirodon, gen. nov.

DERIVATO NOMIS: From Greek *krater* (cup), *kheiros* (hand), and *odon* (tooth) in reference to the resemblance of the teeth to a cupped hand.

TYPE SPECIES: *Kraterokheirodon colberti*, sp. nov. (by monotypy).

GENUS DIAGNOSIS: As for the type and only known species that follows.

Kraterokheirodon colberti, sp. nov.

SYNONYMY: “undescribed traversodontid” Murry and Long, 1995 (p. 56)

1995 “undeterminate traversodontid” Long and Murry, p. 215.

DERIVATIO NOMINIS: In memory of the late Dr. Edwin Colbert, who made many important contributions to Late Triassic vertebrate paleontology.

HOLOTYPE: PEFO 9984, partial tooth lacking root and one side of the crown (Fig. 3F–3J).

TYPE HORIZON AND LOCALITY: Middle portion of Petrified Forest Member, Chinle Formation. Specimen from locality PFV 34, within the Painted Desert region of Petrified Forest National Park, Arizona. Age: Late Triassic (early–middle Norian).

REFERRED SPECIMENS: AMNH 4947, cast of tooth with complete crown and partial root (Fig. 3A–3E).

SPECIES DIAGNOSIS: Tooth differing from all other known vertebrate teeth in possessing a convexly arched transverse ridge of six cusps. Cusp I is the largest and teardrop-shaped in cross-section, cusp II is the smallest, and cusps III through VI are subequal in size in cross-section. Cusps IV through VI are angled labially. The base of the tooth crown possesses a ?posterior shelf extending from the base of the crown.

Description

Unfortunately, the original specimen of AMNH 4947 could not be located despite extensive searches, so a cast was used for this study. Therefore, although PEFO 9984 is a less complete specimen, it has been designated the holotype of *Kraterokheirodon colberti*. Nevertheless, AMNH 4947 is described first because of its more complete nature.

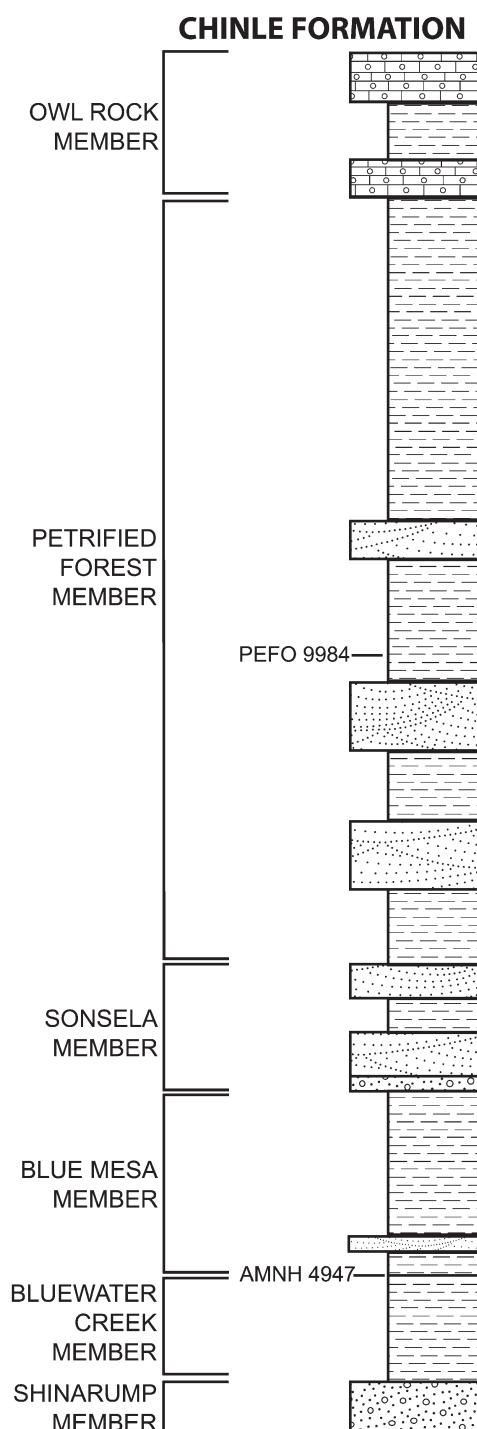
Because of the enigmatic affinities of these teeth (see “Discussion”), it is unclear how they were oriented in the jaw of the animal. In this paper, the shelf on the base of the tooth is arbitrarily considered posterior, and the ridge of cusps is considered anterior. The crown is therefore arranged transversely across the tooth, and the cusps are labeled I through VI. Cusp I is the largest and is considered to represent the lingual margin of the tooth. The teeth are illustrated (Fig. 3) as if they are part of the lower dentition.

AMNH 4947

This tooth consists of a nearly complete crown and the upper portion of the root (Fig. 3A–3E). The tips of the cusps appear to be broken, and the rest of the root is certainly broken off.

The crown is tall and transversely broad. It is slightly arched, with the convex margin to the presumed anterior side of the tooth (Fig. 3E). This ridge is surmounted by six cusps, with corresponding vertical ridges that extend partway down the crown on both the anterior and posterior sides (Fig. 3A, 3B). The presumably lingualmost cusp, cusp I, is the largest, with a labiolingual width of 12.5 mm. In occlusal view, it is teardrop-shaped (Fig. 3E), with the point of the teardrop being the presumed labial margin of the cusp. Cusp II is the smallest, with a labiolingual width of 4.8 mm, although it represents the tallest preserved portion of the crown. Its vertical ridge quickly pinches out between those of cusps I and III (Fig. 3B). As with cusps III through VI, cusp II is ovoid in occlusal view. Cusp III is the second largest cusp, with a labiolingual width of 8.1 mm. Its vertical ridge extends down to the base of the crown; the only cusp to do so. Cusps IV, V, and VI have labiolingual widths of 5.4 mm, 6.0 mm, and 5.5 mm, respectively. Their vertical ridges angle labially, unlike cusps I–III. As the tooth is preserved, these

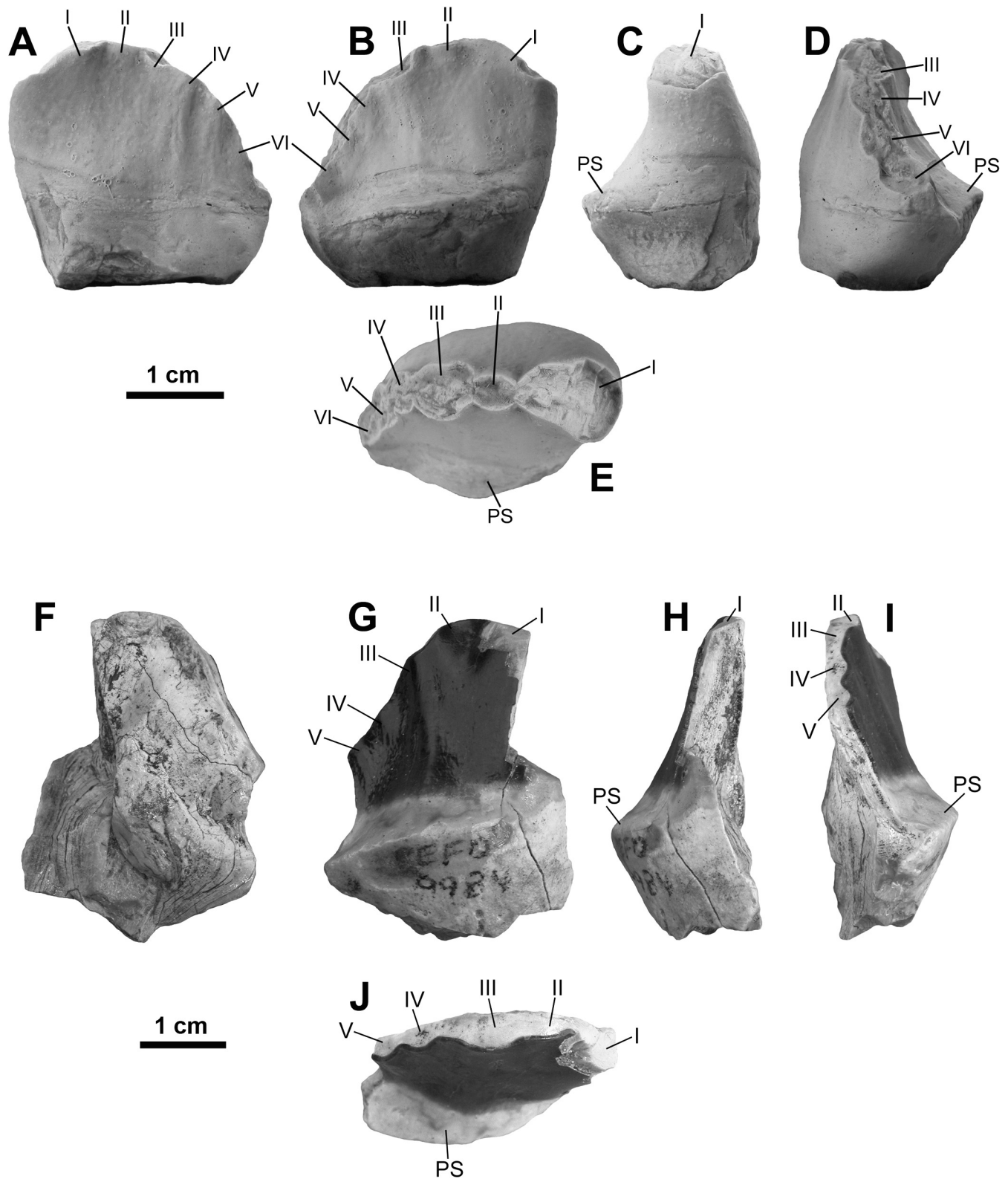
Fig. 2. Composite stratigraphic section of the Chinle Formation in the vicinity of Petrified Forest National Park and St. Johns, Arizona, USA, showing the approximate stratigraphic level for each specimen (redrawn and modified from Heckert and Lucas 2002).



cusps progressively decrease in vertical height, and they curve slightly posteriorly in arrangement. The crown reaches a maximum width of 27.7 mm near its base.

The crown expands posteriorly to form a posterior shelf (Fig. 3C–3E). This shelf is interpreted to be the base of the

Fig. 3. Teeth of *Kraterokheirodon colberti*, gen et sp. nov. Cast of referred specimen AMNH 4947 in (A) anterior view, (B) posterior view, (C) lingual view, (D) labial view, and (E) occlusal view. Holotype specimen PEFO 9984 in (F) anterior view, (G) posterior view, (H) lingual view, (I) labial view, and (J) occlusal view. I–VI, tooth cusps I through VI; PS, posterior shelf.



crown because it does not possess any finished enamel (based on a distinct line on the cast and comparison with PEFO 9984). The shelf angles slightly basally to the labial side of the tooth. On the anterior side of the tooth, the crown constricts slightly where it meets the base of the tooth. Basal to the posterior shelf, the base of the tooth constricts gradually, until it terminates in the broken end. In basal view, the base of the tooth is labiolingually wide and oval in cross section, with a width of 21.0 mm.

PEFO 9984

This specimen consists of a partial crown and a portion of the base of the tooth (Fig. 3F–3J). The entire anterior face of the tooth has broken away, exposing the internal structure of the tooth (Fig. 3F). The dark material on the posterior surface of the crown is enamel, with the rest of the tooth composed of dentine. The labial and lingual margins of the tooth are also broken, so that part of cusp I and all of cusp VI are missing (Fig. 3H, 3I). Unlike AMNH 4947, the natural occlusal margin of the crown is preserved (Fig. 3J).

Although less complete than AMNH 4947, the preserved portions of PEFO 9984 are identical morphologically. The preserved labiolingual width of cusp I is 6.5 mm, although incomplete. The width of cusp II, the smallest cusp, is 3.4 mm. Cusp III is 8.2 mm wide labiolingually, and its vertical ridge extends down to the edge of the crown, as in AMNH 4947. Cusp IV is 5.2 mm wide, cusp V has an incomplete preserved width of 4.5 mm, and cusp VI is not preserved. As in AMNH 4947, cusps IV and V are angled labially. Between the vertical ridges of the cusps, the enamel of the crown displays an anastomosing texture of fine ridges < 0.3 mm wide. The crown has a maximum height of 19 mm and a maximum preserved width at its base of 25.2 mm. The occlusal surface shows wear that is perpendicular to the crown, and much of the finished enamel has worn off (Fig. 3J). Only cusps I and III show slight angulation of this wear posteriorly. The nature of the tooth wear suggests that tooth-to-tooth occlusion occurred between the upper and lower jaws of this animal. The posterior shelf at the top of the base of the tooth is identical to that seen in the AMNH 4947.

Discussion

Although novel in form, these specimens are clearly teeth and not some other element (e.g., chondrichthyan dermal denticle) because they possess the full complement of dentine, enamel, a root, and a clear occlusal surface (on PEFO 9984). The present teeth are so unique in their morphology that confident assignment to any known group of vertebrates is impossible. Certain features do suggest a possible affinity with the Synapsida; however, such resemblances are superficial at best.

Kraterokheirodon bears little resemblance to any known Triassic basal vertebrate. Toothplates from dipnoans, such as the widespread Late Triassic form *Arganodus*, do possess multiple ridges with pointed tips (Murry 1989), but these are oriented mediolaterally within the jaw and only bear a vague resemblance to the present teeth. Furthermore, dipnoan teeth do not have discrete roots and show simple acrodont tooth implantation. Some teleosts possess large, anterior grasping teeth that bear a slight resemblance to *Kraterokheirodon*,

however the absence of acrodine caps on the teeth of *Kraterokheirodon* precludes them from being actinopterygian (Janvier 1996) and thus teleost. Neither do the teeth bear any resemblance to basal tetrapods, which generally have simple homodont dentitions of conical teeth. Additionally, most large temnospondyls known from the Late Triassic have teeth with labyrinthodont internal structure, and this is not present in *Kraterokheirodon* (Hunt 1993).

Several features strongly suggest amniote affinities for *Kraterokheirodon*. Complex, multicusped teeth are a feature of many lineages within the Amniota. The large bases of the teeth, although broken, indicate that a large root was present. The finished surface at the base of the crown and top of the root show that the teeth did not fuse to the jaw. This means that *Kraterokheirodon* probably had thecodont tooth implantation — a common feature of many amniotes, especially synapsids and archosaurs. Finally, of all the teeth surveyed, *Kraterokheirodon* shows the closest similarities to those found within the Amniota.

Multicusped teeth have evolved several times within amniote lineages. Mesozoic groups include the Procolophonidae (Spencer and Storrs 2002), Sphenodontia (Fraser 1988), various basal archosauromorphs (Gregory 1945; Sues 2003), Crocodylomorpha (Clark et al. 1989; Buckley et al. 2000), Pterosauria (Wild 1984), Dinosauria, and Synapsida (including mammals). However, whereas some of the multicusped members of these clades share vague similarities with *Kraterokheirodon*, only members of the Synapsida are close enough in morphology to consider any type of phylogenetic relationship.

One particular group within the Synapsida does show remarkable similarities with the present teeth, the “traversodont” cynodonts. This paraphyletic group (Hopson and Kitching 2001) possesses unique, easily distinguishable teeth that are often diagnostic to species level (Crompton 1972). Tooth morphology varies between upper and lower jaws, as well as tooth position within the jaw (Crompton 1972). Lower postcanines of “traversodont” cynodonts are particularly reminiscent of *Kraterokheirodon*. In all “traversodonts,” the lower postcanine possesses an anterior ridge of multiple cusps with corresponding vertical cusp bodies, accompanied by a posterior shelf at the base of the crown (Crompton 1972; Hopson 1984). The resemblance with the Chinle teeth is especially striking when one compares them with the lower postcanines of *Arctotraversodon* from the Late Triassic of Nova Scotia (Hopson 1984, fig. 10; Sues et al. 1992). Both *Kraterokheirodon* and *Arctotraversodon* share the features listed earlier in the paragraph, and in general morphology are quite similar.

Despite the gross similarity, important differences remain. Although size alone is not a useful phylogenetic character, it is worth noting that the *Arctotraversodon* postcanine tooth is much smaller than the Chinle teeth. The anterior ridge in “traversodont” postcanines never has more than two or three cusps, with a variable number of small accessory cusps (Sues and Olsen 1990; Sues et al. 1992; Sues et al. 1999). In *Kraterokheirodon*, there are six cusps, with only one that could be considered an accessory cusp (cusp II). Furthermore, the cusps in “traversodonts” are nearly parallel to each other, whereas in *Kraterokheirodon* several of the cusps (IV–VI) are angled within the vertical plane. Also, in *Arcto-*

traversodon, the two largest cusps are the most lingual and labial cusps (Hopson 1984, fig. 10). In *Kraterokheirodon*, the two largest cusps are the lingualmost cusp (I) and the middle cusp (III). Finally, and most strikingly, the enamel, which defines the crown, covers the posterior shelf in “traversodonts” (including *Arctotraversodon*) (Crompton 1972; Hopson 1984) but does not reach the shelf in *Kraterokheirodon*. It is possible that this is owing to wear, however the precise occlusion of the teeth indicated by the occlusal surface in PEFO 9984, and the fact that there is a lack of enamel on both specimens, suggests this is unlikely.

Godefroit and Battail (1997) described an extensive cynodont assemblage from the Late Triassic of France. Some of the taxa are grossly similar to *Kraterokheirodon* in possessing multiple cusps, but they differ in their much smaller size, lack of a convexly arched crown, having no posterior shelf, and no occlusal surface wear pattern. Possible cynodont teeth described by Heckert (2004) also lack these features. Lucas et al. (1999) described several teeth from the latest Triassic of New Mexico as cynodonts. Although they are not particularly similar to *Kraterokheirodon*, they are also uncharacteristically large for cynodont teeth. However, these New Mexico specimens may not be from synapsids (H.-D. Sues, personal communication, 2005). Interestingly, Lucas et al. (1999, p. 333) describe “fine ridges and valleys that run from the tip toward the base of the crown.” This enamel pattern is very similar to the anastomosing ridges on the enamel of PEFO 9984, although it is not clear if they have any phylogenetic significance.

All of this makes phylogenetic placement of *Kraterokheirodon* decidedly problematic. Although one could cite certain characters as synapomorphies linking it with “traversodont” cynodonts (e.g., multiple cusps in a transverse row (Hopson and Kitching 2001)), the major differences outlined earlier in the text suggest that homology of these features is at best uncertain. The possibility of synapsid affinities for the teeth is intriguing, but considering the likelihood of convergent morphology we choose at present to only refer the teeth to the clade Amniota. Examination of the microstructure of the teeth under thin section could clarify the possibility that they are from synapsids (Sander 1997), but we refrain from destructive sampling of the holotype. Referral to the Synapsida, without specifically referring the teeth to Cynodontia, would not make sense because only therocephalians and cynodonts have comparable multicusped teeth. While the teeth do show some characteristics in common with “traversodont” cynodonts, these are overshadowed by several important differences that bring into question whether the similarities are truly homologous or just analagous. Teeth in jaws and other non-dental elements must be found before a more certain phylogenetic placement is possible.

Most importantly, the recognition of these teeth as a new and unique taxon is a reminder of how little is still known about the fauna of the Late Triassic Period. Although the Chinle Formation in Arizona has been studied geologically and paleontologically for nearly 100 years, the existence of *Kraterokheirodon* shows that our knowledge of the vertebrate faunal diversity of the Late Triassic of western North America is relatively poor. *Kraterokheirodon* represents a previously unknown large tetrapod that has gone undocumented in the continental Triassic record.

Acknowledgments

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